# A GIANT EXTINCT INSECTIVORE FROM CUBA (MAMMALIA:INSECTIVORA:SOLENODONTIDAE)

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Abstract.—A femur, identified as that of a previously unknown giant solenodontid insectivore, is reported from a fossil deposit in Cuba containing a typical Greater Antillean late Pleistocene mammalian fauna. The fossil is closest in morphology to *Solenodon cubanus* among known insectivores Lack of adequate material precludes description of a new taxon, although the femur probably represents an undescribed species of *Solenodon*. Based on measurements of the femur, the giant Cuban solenodontid would have been considerably larger than any living member of the Insectivora. Addition of a new very large insectivore suggests a substantial radiation of insectivores in the Greater Antilles, similar to that of capromyid rodents and of megalonychid sloths.

This report is based on a partial femur (USNM 299480) from western Cuba belonging to a previously unknown mammal. The specimen was collected on 15 March 1959 by Oscar Arredondo and César García del Pino from the Abra de Andrés, Las Alturas de Esperón, Mesa de Anafe, Sierra del Rosario, near the city of Guanajay, Pinar del Río Province, Cuba. According to the new geographic subdivision of Cuba, this locality is now in Habana Province, but because maps showing the new Cuban provinces are not generally available at present, we will use the more conventional boundaries and names of the Cuban provinces. The femur was collected from a reddish-colored breccia deposited in a crevice in a rock wall of Miocene age. A late Pleistocene age is suggested for the breccia based on the vertebrate fossils collected from it. The associated vertebrate fauna includes three species of small megalonychid ground sloth, Megalocnus rodens, Mesocnus sp. and Neocnus gliriformis (for use of Neocnus rather than its synonyms Microcnus and Cubanocnus see Varona, 1976), and two species of capromyid rodent, Geocapromys columbianus and Capromys sp. (either C. pilorides or C. prehensilis). All of these species have been recovered from late Pleistocene cave deposits elsewhere in Cuba and, with the exception of Capromys, all are now extinct. Although much paleontological field work has been conducted throughout Cuba during the past 20 years, no additional specimens referable to this unique mammal have yet come to light.

Description of femur.—The fossil femur which is the subject of this study lacks the head, much of the lesser trochanter, and the medial condyle (Fig.

1). It is relatively short and massive with a prominent greater trochanter, third trochanter, trochanteric fossa, and intertrochanteric crest. The femoral shaft is straight for most of its length, but is flexed slightly anteriorly near the proximal end. The shaft is nearly hemicircular in cross section, convex on the anterior surface and almost flattened on the posterior surface. The greater trochanter appears to have projected approximately 4-5 mm above the femoral head and is separated from the head by a deep groove on the anterior surface. In anterior aspect, the greater trochanter is broad at its base narrowing proximally to a relatively sharp prominence. On the anterior surface of the greater trochanter just distal to the proximal end there is a small, transversely elongate protuberance, presumably for attachment of the gluteus minimus. In lateral view, the greater trochanter is flexed somewhat anteriorly and is broadly rounded proximally. The trochanteric fossa is well developed, forming a very deep pit in the posterior surface of the greater trochanter. The intertrochanteric crest is prominent and composed of two portions; the anterior part is a thin ridge of bone arising at the tip of the greater trochanter and forming the posterior border of the trochanteric fossa and the distal portion of the crest is transverse to the shaft and is gently concave. The vertical and horizontal portions of the intertrochanteric crest meet at nearly a right angle (85°) just proximal to the third trochanter. Although broken off near its base, the lesser trochanter appears to have been strongly developed and to have met the medial edge of the shaft at approximately a right angle. The lesser trochanter is located slightly higher on the shaft than is the third trochanter. The third trochanter is a very prominent triangular-shaped process which extends about one-sixth the length of the femur. On the distal end, the patellar groove, although partially missing, is relatively narrow, slightly concave, and projects anteriad of the femoral shaft. Proximal to the patellar trochlea there is a deep pit for reception of the patella during strong extension of the leg. The distal end of the femur is deep anteroposteriorly, but is not particularly broad. The articular surface of the lateral condyle is vertical and relatively narrow, whereas the intercondylar notch is comparatively broad.

*Comparison with other mammals.*—Although incomplete, this specimen retains enough diagnostic features to permit detailed comparisons with other mammalian groups. We have compared the fossil femur with femora of representative genera of all orders of native mammals known from the late

Fig. 1. A, C, E, G.—Posterior, anterior, lateral, and medial views of giant solenodontid femur from the Abra de Andrés, near Guanajay, Pinar del Río Province, Cuba (USNM 299480); B, D, F, H.—Posterior, anterior, lateral, and medial views of the left femur of *Solenodon cubanus* (USNM 49508). All views  $\times^{7}/_{6}$ .



Pleistocene and modern fauna of the West Indies. Only the Marsupialia, Insectivora, Chiroptera, and Rodentia are represented in the contemporary fauna of the West Indies. Primates and Edentata are added when late Pleistocene faunas are included. Specimens from the following collections were used in this study: National Museum of Natural History (USNM), Carnegie Museum of Natural History (CM), Florida State Museum (UF), and the personal collection of Oscar Arredondo (OA).

The femora of Chiroptera can be excluded from further consideration for obvious reasons such as their small size, very slender shaft, and highly derived morphology of the proximal end. The only marsupials in the West Indies are the didelphid genera Didelphis and Marmosa, both known in this region only from the Lesser Antilles. The femur of these marsupials is quite different from that of the fossil. The femoral shaft is much longer and more slender, the third trochanter is virtually absent, the greater trochanter extends only slightly proximal to the head, and the patellar trochlea is very broad, as is the articular facet of the lateral condyle. Many features of the femora of New World monkeys, the elongate shaft, reduced third trochanter located in a more proximal position, and the comparatively broad patellar trochlea, preclude placement of the fossil in the Primates. In the rodent femora examined, the lesser trochanter is located primarily on the posterior surface of the femoral shaft, the third trochanter is vestigial and located far distal to its position in the fossil, and the patellar groove is much deeper. Small, extinct ground sloths of the family Megalonychidae are the only representatives of the Edentata in the West Indies. The femur in these small sloths differs strikingly from that of the fossil in such features as the relative proportions of the shaft, the weak development of the greater and lesser trochanters, trochanteric fossa, and intertrochanteric crest, and the shape of the patellar groove. Only in the femora of certain genera in the order Insectivora can a reasonably close match be found for the Cuban fossil femur.

Femora of all living insectivore families were available for study, with the number of genera examined for each family following it in parentheses: Solenodontidae (1), Tenrecidae (7), Chrysochloridae (4), Soricidae (11), Talpidae (7), and Erinaceidae (7). Following Butler (1972) and McKenna (1975) the tree shrews (Tupaiidae) and elephant shrews (Macroscelididae) are excluded from the Insectivora (*sensu stricto*, i.e. restricted to the Lipotyphla), but in any case the fossil bears little resemblance to the femora of either group. In addition to living insectivores, the fossil was compared to the femur of *Nesophontes*, the only genus in the extinct Greater Antillean insectivore family Nesophontidae and to the femora of several fossil *Solenodon*-like forms and the extinct solenodontid *Antillogale* (regarded as *Solenodon* by Van Valen, 1967, and Varona, 1974). The fossil Cuban insectivore was also compared to the femur of *Deinogalerix koenigswaldi* 

from the Miocene of Italy, the largest known insectivore, living or extinct (Freudenthal, 1972).

With the exception of one genus of tenrec, the fossil differs considerably from the femora of all tenrecids and chrysochlorids, all of which have the greater trochanter approximately even with or lower than the head, lack a well defined trochanteric fossa and intertrochanteric crest, and have a smaller third trochanter located farther distally on the shaft. The femur of Microgale, one of the smallest genera of tenrecs, is similar to the fossil in morphology, differing only in its considerably smaller size and elongate, flange-shaped third trochanter. The fossil bears little resemblance to the femur of any living talpid or soricid. Besides the obvious discrepancy in size, the femur in moles and shrews lacks a well developed trochanteric fossa and intertrochanteric crest, has the third trochanter located higher on the shaft, and is relatively broader distally. Modern erinaceids are divisible into two subfamilies, the Erinaceinae and Echinosoricinae, which differ significantly in their femoral morphology. Erinaceine femora differ in a number of ways from the Cuban fossil, including having a less pronounced greater trochanter, the trochanteric fossa not as concave, and the third trochanter developed as an elongate flange extending nearly one-third the length of the shaft. The patellar groove in hedgehogs does not extend nearly as far proximally as it does in the fossil and the lateral condyle is somewhat reduced. Among living echinosoricines, the fossil femur resembles most closely the femur of *Echinosorex*, especially in its overall proportions and in the strong development of the greater trochanter, third trochanter, and trochanteric fossa. However, the morphology of the distal end of the femur in Echinosorex is like that of other erinaceids and quite unlike the Cuban fossil. The femur of the gigantic extinct echinosoricine Deinogalerix is very similar in most respects to the femur of Echinosorex, except, of course, for its tremendous size. As with Echinosorex, several fundamental differences in the distal end of the femur argue against a close relationship between Deinogalerix and the Cuban specimen. Nonetheless the femora of these two giant insectivores are quite similar in gross morphology, particularly in their long, relatively gracile (for an insectivore) overall form and the strongly developed greater trochanter, third trochanter, and trochanteric fossa.

As was suspected on the basis of geography, the fossil bears a closer resemblance to the femora of the West Indian insectivores *Solenodon* and *Nesophontes* than it does to those of any other living insectivores. Although there are some minor differences, the femora of these two genera are more similar to one another than either is to that of any other living insectivore. The differences in postcranial osteology between these two genera are less pronounced, for instance, than the differences observed between certain genera within the Tenrecidae or Erinaceidae. McDowell (1958) summarized the many similarities in the cranial and postcranial osteology of *Solenodon* 

and *Nesophontes* and hypothesized a close phylogenetic relationship between them, placing both genera in the Solenodontidae. However, the profound differences in dentition between *Solenodon* and *Nesophontes* seem to preclude their placement in the same family, at least in the present state of our knowledge of insectivore relationships. The possibility does exist that the Solenodontidae and Nesophontidae are closely related within the soricomorph insectivores and may even have been derived from a single "invasion" of the West Indies or "proto-Antilles" by a late Cretaceous or early Tertiary soricomorph (MacFadden, in press).

Comparison with Solenodon, Nesophontes, and Antillogale.—To determine if the fossil femur is closest in morphology to Solenodon, Antillogale, or Nesophontes, the fossil was compared to the femora of all living and extinct West Indian insectivores for which the femur is known. These include, Solenodon cubanus and several large Solenodon cubanus-like forms, all from Cuba, S. paradoxus and Antillogale marcanoi from Hispaniola, and six species of Nesophontes, three from Hispaniola and one each from Puerto Rico, Cuba, and the Cayman Islands.

The most striking feature of the fossil femur is its large size. It is 27% longer than the longest modern Solenodon femur measured (Table 1) and is considerably larger than the femur of any living insectivore. Aside from the obvious difference in size, the largest Nesophontes being barely half the size of Solenodon or Antillogale, the femur of Nesophontes differs consistently from those of the latter two genera in several features. Antillogale and Solenodon are certainly closely related, if not congeneric, and in femoral morphology they are quite similar. In the following comparison of femoral characters in Nesophontes and Solenodon, the characters ascribed to Solenodon apply also to Antillogale, unless noted otherwise. In Solenodon the lateral condyle is transversely flattened, in contrast to its convexity in Nesophontes. The patellar groove of Solenodon projects anteriad of the shaft, unlike Nesophontes in which the patellar trochlea is in line with the axis of the femoral shaft. Solenodon has a deep pit on the anterior surface of the shaft just proximal to the patellar groove, for reception of the patella in strong extension of the lower leg. This pit is very weakly developed in the large species of Nesophontes, N. edithae, and is absent in the smaller species. In all Solenodon specimens examined, the third trochanter is more strongly developed than in any species of Nesophontes and is located slightly higher on the shaft. The lesser trochanter is of slightly different shape in the two genera, pointed and projecting at a right angle from the shaft in Nesophontes and triangular, relatively broader, and projecting somewhat proximally in Solenodon. The femur of Solenodon has a longer neck and a slightly oblong head, whereas the neck is shorter in Nesophontes (owing at least in part to the relatively larger head) and the head is almost perfectly hemispherical. The greater trochanter in Solenodon exhibits a strong an-

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	Total length	Shaft length	Maximum proximal width	Height of greater trochanter	Minimum shaft width	Minimum shaft thick- ness	Maximum shaft width at third trochanter	Maximum width of condyles	Maximum distal width	Maximum distal thickness	Width of patellar groove	Index of robustness minimum shaft width/ total length
giant fossil solenodontid (USNM 299480)	66.1	60.4	I	4.5	7.1	6.2	11.6	I	I	14.4		.107
Solenodon cubanus (USNM 49508)	47.3	43.9	13.3	2.5	4.7	3.8	7.9	11.1	11.8	10.2	6.3	660.
Solenodon cf. cubanus fossil (OA 301)	57.7	46.0	16.0	3.5	6.0	I	9.7	13.6	14.5	12.8	7.0	.104
Solenodon cf. cubanus fossil (OA 2943)	I	.	15.5	3.2	6.3	5.0	9.3	I	I	I	- 1	1
Antillogale marcanoi fossil (CM 35036)	41.2	38.3	12.7	2.1	5.4	4.7	7.6	11.1	12.4	9.6	7.5	.131
Solenodon cf. paradoxus fossil (USNM 299486)	40.0	37.1	12.3	2.2	4.6	4.3	7.6	9.9	11.0	8.2	5.6	.115
Solenodon paradoxus (N = 9) X OR V	46.3 42.7–48.5 4.00	42.9 39.9–45.2 4.31	14.1 13.5–14.6 2.66	2.5 2.2–3.0 12.49	5.3 4.9–5.7 4.37	4.3 3.7–4.8 7.80	8.3 7.5–9.4 7.83	11.6 10.9–12.4 3.97	13.0 12.0–13.6 3.87	9.9 8.9–10.8 5.52	7.0 6.3-7.7 6.04	.114
Nesophontes edithae (N = 20) $\bar{x}$ OR V	23.4 21.1–24.8 4.41	21.9 20.0–23.1 4.30	6.1 5.6–6.5 4.28	1.5 1.2–1.8 11.59	2.7 2.2-3.0 8.17	2.1 1.7–2.3 7.52	3.5 2.9–3.9 8.32	5.0 4.7–5.4 4.42	5.3 4.9–5.7 4.34	4.6 4.1–5.2 5.50	3.1 2.8–3.5 6.93	.113
Nesophontes paramicrus (N = 20) $\tilde{x}$ OR V	17.8 16.5–19.8 4.74	16.7 15.5-18.7 4.55	4.3 4.0-4.7 4.84	1.1 0.9–1.4 11.53	1.7 1.4–2.1 9.15	1.5 1.3-1.7 8.35	2.6 2.3–3.1 7.32	3.4 3.1–3.7 4.45	3.6 3.3–3.9 4.47	3.3 2.9–3.7 6.41	2.0 1.8–2.2 7.03	960.

terior flexion which is not nearly as pronounced in the smaller genus. Finally, there is a difference in the angle formed by the intertrochanteric crest, acute in *Solenodon*, right to obtuse in *Nesophontes*.

Difficulties arise when the fossil is compared to all species of Solenodon and Nesophontes, rather than to generalized characters for the individual genera. Comparisons reveal that there are notable differences between the femora of the species within each of these two genera. For instance, the femur of Nesophontes edithae differs considerably from the femora of the smaller species of the genus, particularly in its relatively larger head, broader patellar groove, and comparatively broader shaft. The index of robustness (minimum shaft width/total length of femur) reveals that the femur of the N. edithae specimens measured is as robust as the femur of Solenodon paradoxus, an animal twice its size. The remaining species of Nesophontes have more slender femora.

Although only one skeleton of modern Solenodon cubanus was available for study, we did examine two fossil femora from western Cuba of a form very close to the modern Cuban solenodon. Solenodon cubanus appears to differ in several important femoral characters from S. paradoxus. The index of robustness demonstrates clearly that the femur of S. cubanus is of more slender build than that of S. paradoxus. Unlike S. paradoxus and like Nesophontes, the greater trochanter in S. cubanus is not flexed anteriorly to a marked degree. The patellar groove in S. cubanus is narrower and less concave than in S. paradoxus and the pit proximal to this groove is shallower in the former.

The femur of Antillogale marcanoi differs from that of S. cubanus and S. paradoxus in several features. The most striking feature of Antillogale is the relative massiveness of its limb elements. Like the humerus and ulna described by Patterson (1962), the femur of Antillogale is similar to that of S. paradoxus in the breadth of the proximal and distal ends, but has a noticeably shorter shaft, giving it a much stouter, more massive appearance. In addition, the femoral shaft of Antillogale has a distinct curvature not observed in other West Indian insectivores. The pit on the anterior surface of the shaft proximal to the patellar groove is deeper and the greater trochanter is flexed anteriorly to a greater degree than in either species of Solenodon. In these last two features and in the relative robustness of the shaft and broad, concave patellar trochlea, the femur of Antillogale more closely resembles that of S. paradoxus than it does the femur of S. cubanus, Nesophontes, or the Cuban fossil.

In almost every aspect of its morphology, the Cuban fossil femur resembles the femur of *Solenodon cubanus* more closely than it does the femur of any other West Indian insectivore (Fig. 1). Although the giant fossil femur does resemble *Nesophontes* more closely in several characters than it does *S. paradoxus*, particularly in the slenderness of the shaft and the reduced

anterior flexion of the greater trochanter, it also shares these characters with S. cubanus. In characters such as the stronger development and the more proximal location of the third trochanter, the angle formed between the shaft and the lesser trochanter, the length of the femoral neck, the angle formed by the intertrochanteric crest, the shape of the lateral condyle, the anterior projection of the patellar groove, and presence of a well defined pit proximal to the patellar groove, the fossil resembles Solenodon more closely than Nesophontes and in particular, resembles S. cubanus more closely than S. paradoxus or Antillogale.

Although the fossil femur is most similar to the femur of Solenodon cubanus among known insectivores, several differences are apparent, the most obvious being one of size. The fossil solenodontid femur is 1.4 times longer than that of modern S. cubanus. The ratio of femur length/head and body length was calculated for three modern individuals of Solenodon paradoxus, the species most closely related to the fossil for which these data are available. The resulting ratio ( $\bar{x} = .14$ ) suggests a head and body length for the fossil solenodontid of approximately 470 mm. This is about the size of a large adult male opossum (Didelphis virginiana), and is considerably larger than any living member of the Insectivora. There are several fossil Solenodon cf. cubanus femora from western Cuba which are intermediate in size between modern S. cubanus and the giant solenodontid (Table 1). These specimens are very similar to S. cubanus, differing primarily in their larger size. Based on the available fossil material, it is not clear if these intermediate-sized specimens represent a third late Pleistocene solenodontid species or are representative of a late Pleistocene population of S. cubanus which was larger than the modern form. Other characters which distinguish the giant solenodontid from S. cubanus are the more prominent greater trochanter, deeper trochanteric fossa, better developed groove separating the head from the greater trochanter, larger third trochanter, and slightly concave lateral condyle. Most of these characters are not unique to the giant solenodontid, but rather are characters found developed to a lesser degree in Solenodon cubanus. It is possible that the observed differences are related to the large size of the fossil, but this cannot be determined from the limited material available.

In summary, the giant insectivore femur can be assigned confidently to the Solenodontidae. In morphology it agrees closely with *Solenodon*, in particular with *S. cubanus*, to which the fossil appears to be most closely related among known insectivores. This specimen almost certainly represents an undescribed species, tentatively assignable to the genus *Solenodon*, but the incomplete femur described here does not provide adequate material for the formal description of a new taxon.

Discussion.—The presence in the late Pleistocene fauna of Cuba of a giant solenodontid, larger than any living insectivore, raises some intriguing ques-

tions regarding its ecological position in that fauna. Based on the carnivorous habits of its closest living relatives, it seems likely that the giant Cuban solenodontid was also carnivorous, at least in part. Certainly Solenodon paradoxus eats small mammals, lizards, and frogs, in addition to various invertebrates (based on observations of captive S. paradoxus by C. E. Ray and others; see also Allen, 1910; Peña, 1977; Verrill, 1907), so it is not inconceivable that a very closely related animal of considerably larger size would have preyed on small to medium-sized vertebrates. Taken in the context of the entire Cuban fauna, the carnivorous habits of Solenodon and possibly the giant solenodontid may reflect the absence of other mammalian predators. In the absence of members of the Carnivora, the majority of carnivorous niches in Cuba are filled by nonmammalian predators. The largest native carnivorous vertebrates on Cuba today are the boa, Epicrates angulifer, several species of medium-sized raptorial birds, and Solenodon cubanus. The inclusion of late Pleistocene faunas would add the gigantic flightless owl, Ornimegalonyx oteroi, two species of giant barn owl, the extinct eagle, Aquila borrasi, and possibly the giant solenodontid.

Absence of members of the Carnivora from Cuba invites comparison with other well known faunas in which carnivores (i.e. Carnivora) are absent. In the near absence of Carnivora in the Tertiary of South America (with the exception of procyonids in the Neogene) an impressive array of carnivorous marsupials and large flightless predaceous birds is found (Marshall, 1977). In Australia there evolved a full complement of marsupial carnivores and the titanic varanid lizard, Megalania, in addition to several other mediumto large-sized carnivorous varanids (Hecht, 1975). There are, however, no members of the Insectivora in either of these faunas (with the minor exception of small shrews of the genus Cryptotis in the modern fauna of northernmost South America). Olson (1978) noted the striking parallel between the Miocene fauna of the Gargano Peninsula of Italy (Freudenthal, 1972) and that of the late Pleistocene of Cuba. The Gargano Peninsula was apparently an island in the Miocene and during that time its faunas are characterized by the virtual absence of carnivores (with the exception of an otter of remarkably large size) and by the presence of several species of large raptorial birds, the largest known insectivore, Deinogalerix koenigswaldi, and rodents of very large size (Freudenthal, 1972). The virtual absence of mammalian carnivores and the presence of a giant insectivore and very large raptorial birds mirrors the situation in Cuba during the late Pleistocene. Giant rodents are unknown from Cuba, but the small Cuban ground sloths may have occupied a similar niche. It is probably no coincidence that the giant Cuban solenodontid and Deinogalerix, the largest of known insectivores living or extinct, both occur in faunas devoid of other mammalian predators. Competition from more advanced predators of the Carnivora has

probably prevented modern insectivores from attaining the large size of these two fossil forms.

The giant solenodontid described here, in addition to recently discovered species of Nesophontes from Puerto Rico, Vieques, Cuba, and the Cayman Islands, provides evidence to support our conviction that the Quaternary vertebrate fauna of the West Indies is at present incompletely known. Furthermore, the lack of terrestrial vertebrate fossils in the West Indies older than the late Pleistocene strongly indicates that there is still much to learn about the Greater Antillean insectivore fauna. If the Greater Antillean insectivores were derived from North American early Tertiary soricomorphs as suggested by most authors (MacFadden, 1980; Matthew, 1918; Patterson, 1962; Simpson, 1956), we might justifiably expect an insectivore radiation similar to that of another soricomorph group apparently isolated on an island since the early Tertiary, the Tenrecidae of Madagascar. Rather extensive radiations of capromyid rodents, including eight endemic genera and at least 15 species, and megalonychid ground sloths, including seven endemic genera and eight species, have been documented in the Greater Antilles. Both of these radiations have probably taken place since the early Miocene. With the addition of a new species of solenodontid we now know of three genera and at least a dozen species of endemic Antillean insectivores. These figures compare with 12 genera and approximately 25 species of tenrecs on Madagascar, an island about five times larger than Cuba and of considerably greater ecological diversity than any West Indian island. The discovery of a giant solenodontid on Cuba raises the possibility that an even more extensive radiation of insectivores remains to be discovered in the West Indian fossil record.

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#### ADDENDUM

Arredondo and Varona (1974. Poeyana 131:1–12) described a new genus and species of extinct canid, *Cubacyon transversidens*, based on a partial maxilla with two teeth from a cave deposit in Cuba. Olson (1978) questioned the validity of this species and Hall (in press. The Mammals of North America, 2nd Ed., The Ronald Press, New York) synonymized it with the domestic dog, *Canis familiaris*. Morgan and Ray follow Hall in regarding *Cubacyon* as a domestic dog. Arredondo and Varona (1974; in litt.), however, believe that *C. transversidens* is a valid species based on the configuration of the P<sup>3</sup> and M<sup>1</sup> and by its association in a fossil deposit with extinct mammals. Therefore, any comments in this paper regarding the absence of endemic Carnivora on Cuba are the opinion of Morgan and Ray, whereas Arredondo regards *Cubacyon* as part of Cuba's late Pleistocene fauna.